

This article is from the
July 2003 issue of

plant disease

published by
The American Phytopathological Society

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Fire Blight Management in the Twenty-first Century

Using New Technologies that Enhance Host Resistance in Apple

Fire blight has been known as a destructive disease of apple and pear for over 200 years (3). The disease is caused by the bacterium *Erwinia amylovora*, which is capable of infecting blossoms, fruits, vegetative shoots, woody tissues, and rootstock crowns (Fig. 1). There are several distinct phases of the disease including blossom blight, shoot blight, and rootstock blight. The diversity of host tissues susceptible to infection, combined with the limited number of management tools available to control the disease, has made it difficult to stop or slow the progress of fire blight epidemics.

Effective management of fire blight requires an integrated approach of several practices that are aimed at (i) reducing the amount of inoculum that is available to initiate new infections, (ii) imposing barriers to successful establishment of the pathogen on the host, and (iii) reducing host susceptibility to infection (1,55). Most fire blight management strategies developed during the twentieth century focused on the reduction of inoculum in the orchard and the use of antimicrobial treatments to prevent infection. Although increasing host resistance has been recognized as an important component of fire blight management, its application has been limited by a lack of resistant cultivars suited to com-

mercial needs and by a lack of management practices that could effectively increase resistance.

Recent advances have made it feasible to change this paradigm in the twenty-first century. First, apple rootstock breeding programs have developed size-controlling (often dwarfing) rootstocks that are resistant to fire blight and are currently becoming available for commercial use (43). Second, genetic engineering of commercial apple cultivars for increased fire blight resistance has been demonstrated, and transgenic apple plants are now undergoing field trials (2). Third, chemical treatments that enhance host resistance have been demonstrated to be useful in the control of fire blight (9,33,61). Although these technologies are at the early stages of development and are either not available or not proven in the marketplace, incorporating the use of host resistance into fire blight management strategies has become a realistic goal in the twenty-first century. This article describes recent progress in the development of new fire blight control technologies that enhance host resistance by chemical or genetic means.

Current Fire Blight Management

Current fire blight management strategies rely upon phytosanitary measures to reduce inoculum in the orchard and the use of spray treatments to prevent infection, especially blossom infections. Reducing primary inoculum in the orchard by removing holdover cankers during winter pruning was established as a critical component of fire blight management strategies early in the twentieth century (47). Management strategies also include the application of copper sprays at the silver- or green-tip growth stage to reduce primary inoculum in the orchard and the pruning of early-season infections after bloom to reduce the amount of inoculum available for shoot infection (55).

The prevention of the blossom blight phase of the disease is another critical

component of fire blight management, and significant progress was made in our ability to control blossom blight during the late twentieth century. Research demonstrated that the establishment of epiphytic populations of *E. amylovora* on the stigma is a critical step in blossom infection (36,51,58). Several models based on climatic and phenological data were developed to predict the occurrence of fire blight infection periods during bloom, thus improving our ability to control this phase of the disease by the timely application of antibiotic sprays (6,48,49,53). Although blossom blight control has relied heavily on the use of antibiotic sprays to prevent infection, progress was also made in the biological control of blossom infection, and some biological control products are now commercially available (50,59).

Despite this progress, fire blight remains a difficult disease to control. Properly timed applications of streptomycin during bloom can provide over 90% control against streptomycin-sensitive strains of the pathogen; yet failure to control blossom blight remains common for several reasons. Long periods of rainy weather, or the need to protect large blocks, often prevents the timely application of streptomycin, which in order to be effective must be applied 24 to 48 h before, or 24 h after an infection period. Models sometimes fail to accurately predict infection periods due to either the use of inaccurate weather information or the occurrence of unusual conditions outside normal prediction parameters of the model. Streptomycin-resistant strains of *E. amylovora* have developed in most areas of western North America and in Michigan, reducing the effectiveness of streptomycin in these areas. Although oxytetracycline can be used in areas where streptomycin-resistant strains occur, it has been only partially effective, and there have been no other EPA-labeled alternatives to streptomycin that provide high levels of control. To date, biological control agents have not provided consistently

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Publication no. D-2003-0424-02F

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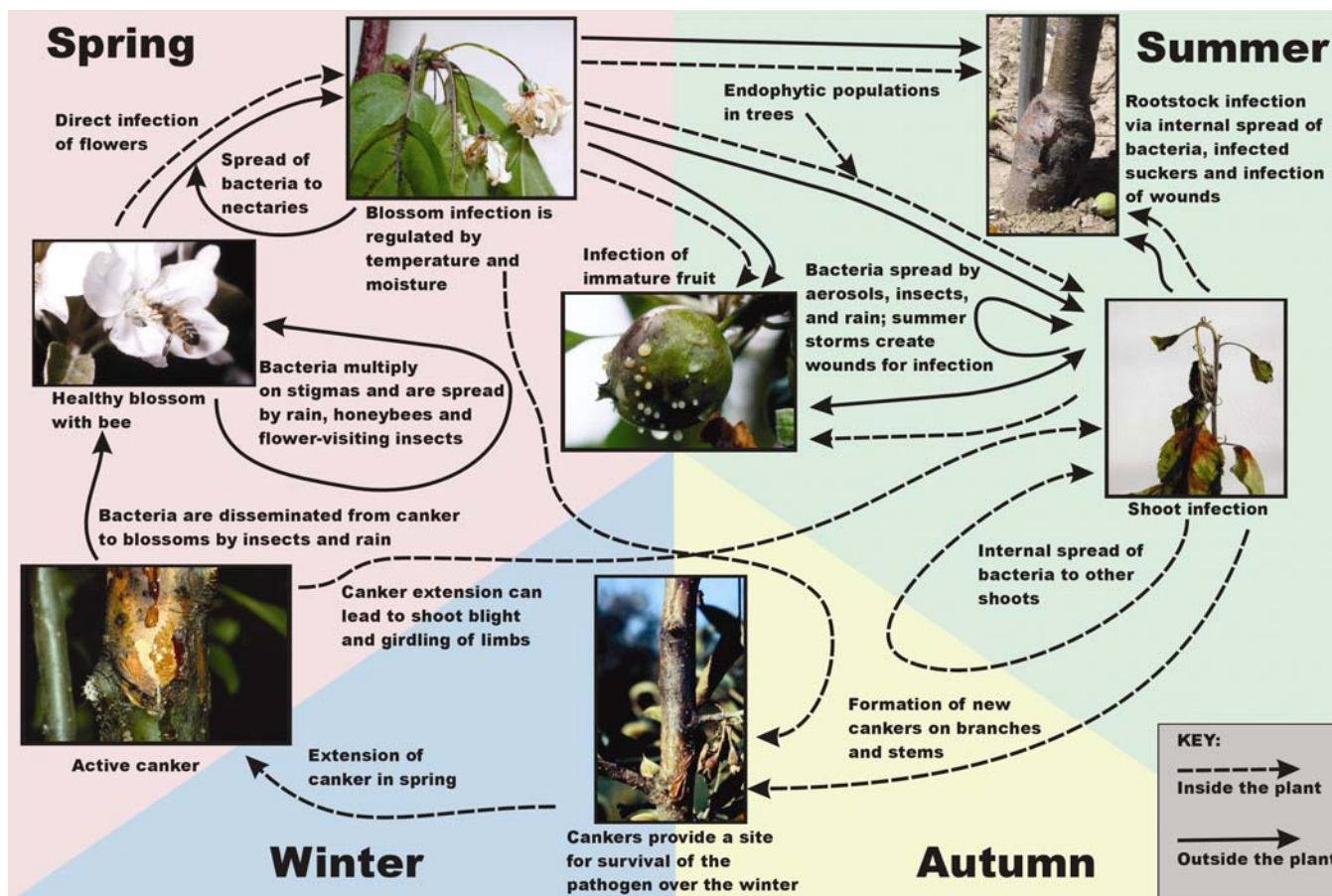


Fig. 1. Disease cycle of fire blight caused by the bacterium *Erwinia amylovora*. Dashed lines represent movement of bacteria and spread of disease within the plant, and solid lines represent movement of bacteria outside the plant. Modified from disease cycle of Sherman Thomson 2000 (52).

high levels of control. In addition, the sporadic nature of fire blight infections and epidemics encourages growers to become lax in implementing costly control practices after several years without serious fire blight outbreaks. If growers fail to control blossom blight, no control strategies have been available to control shoot blight and rootstock blight during the summer months.

The continued threat of fire blight to the pome fruit industry is evident from recent epidemics that have occurred worldwide. A single fire blight epidemic in southwest Michigan in 2000 resulted in the death of over 220,000 trees and the removal of more than 240 ha of apple orchards, with a total economic loss estimated at \$42 million (Fig. 2) (30). Annual losses to fire blight and costs of control in the United States are estimated at over \$100 million. Losses and costs in many other countries, such as New Zealand and Italy in 1998 (56), are also very substantial.

Increased Susceptibility of Apple to Fire Blight

Pear has always been considered highly susceptible to fire blight, and the disease has long been the main factor limiting pear production in the eastern United States. In the twentieth century, fundamental changes in the apple industry resulted from the



Fig. 2. A young apple orchard devastated by fire blight in southwestern Michigan in 2000, where initial estimates put total losses at \$42 million.

adoption of high-density orchard systems, and recent planting of susceptible cultivars and rootstocks has increased the danger of fire blight in apple orchards to unprecedented levels. High-density planting systems have several horticultural advantages including improved fruit quality due to

greater light penetration into the tree canopy, higher yields per hectare, increased tree precocity, which results in quicker returns on investment, and more efficient utilization of chemical and labor inputs as a result of reduced tree size. A high-density apple orchard system depends upon the use

of dwarfing rootstocks. The most commonly used dwarfing apple rootstocks, Malling (M.) 9 and M.26, are highly susceptible to *E. amylovora*, and in almost all cases, fire blight infection kills trees by girdling the rootstock (Fig. 3). A 10% incidence of rootstock blight in a 4-year-old high-density planting can result in losses up to \$8,400 per hectare when the costs of tree replacement, lost investment in tree establishment and maintenance, and reduced yields over several years are considered (37). Currently, there are no effective cultural practices or chemical treatments available to protect rootstocks from infection.

Furthermore, most commercially successful apple cultivars introduced in recent years, including 'Braeburn', 'Fuji', 'Gala', 'Ginger Gold', 'Jonagold', and 'Pink Lady', are much more susceptible to fire blight than most older cultivars. The increased planting costs of high-density plantings combined with the extreme fire blight susceptibility of new apple rootstocks and scion cultivars has resulted in devastating financial losses for many apple growers due to fire blight. Many of the orchards lost to fire blight in the 2000 epidemic in Michigan were 2- to 5-year-old high-density orchards that were just coming into production (Fig. 4).

New Genetic Technologies for Fire Blight Resistance

A very limited number of apple cultivars are responsible for a large proportion of annual production. Consumers and supermarkets prize these cultivars for their appearance, quality, flavor, and storability, while growers also value their orchard characteristics and ready market resulting from consumer demand. To retain the desirable characteristics of a fruiting cultivar while introducing disease resistance genes through conventional breeding methods is virtually impossible because of apple's heterozygosity, long generation time, and self-incompatibility. Genetic engineering offers an attractive alternative since it has the potential to provide faster results, resistance genes can be obtained from many sources, the expression of native apple genes can be modified, and the desirable qualities of the transformed cultivar or rootstock can be preserved.

Several researchers, particularly David James at East Malling, UK, pioneered methods to transfer genes into apple (16,25,31). We drew on their work and our own early work to develop efficient *Agrobacterium*-mediated gene transfer protocols for several apple cultivars (8,44). Two scion cultivars of 'Gala' ('Royal Gala' and 'Galaxy') and the rootstock cultivar M.26, all of which are highly susceptible to fire blight, have been used as model cultivars in our research to enhance fire blight resistance by genetic engineering. Depending on the construct being introduced, these cultivars generally yield at least 5 to 10 transgenic lines per 100 leaf pieces transformed, and within about 8 months after the start of a transformation experiment, we can have transgenic plants of apple cultivars and rootstocks available in the greenhouse for disease evaluation (7).

Initially we hypothesized that fire blight resistance in apple would be enhanced by transferring genes for antimicrobial proteins with low toxicity to eukaryotic cells. Genes encoding the antimicrobial proteins attacin E, avian lysozyme, and the cecropin analogs, SB-37 and Shiva-1, were transferred to 'Royal Gala' apple. To date, the highest level of fire blight resistance has been observed with attacin-transgenics, although cecropin- and avian lysozyme-transgenics also had statistically significant increases in resistance (41). Growth chamber and greenhouse trials have demonstrated a positive correlation between attacin content of transgenic plants and their resistance to fire blight (28).

Most bacterial plant pathogens, including *E. amylovora*, multiply in intercellular spaces before causing disease symptoms, so expression of antimicrobial proteins in intercellular spaces close to or at the site of early infection events could be important for their ability to enhance resistance (17). A potential disadvantage of targeting an-

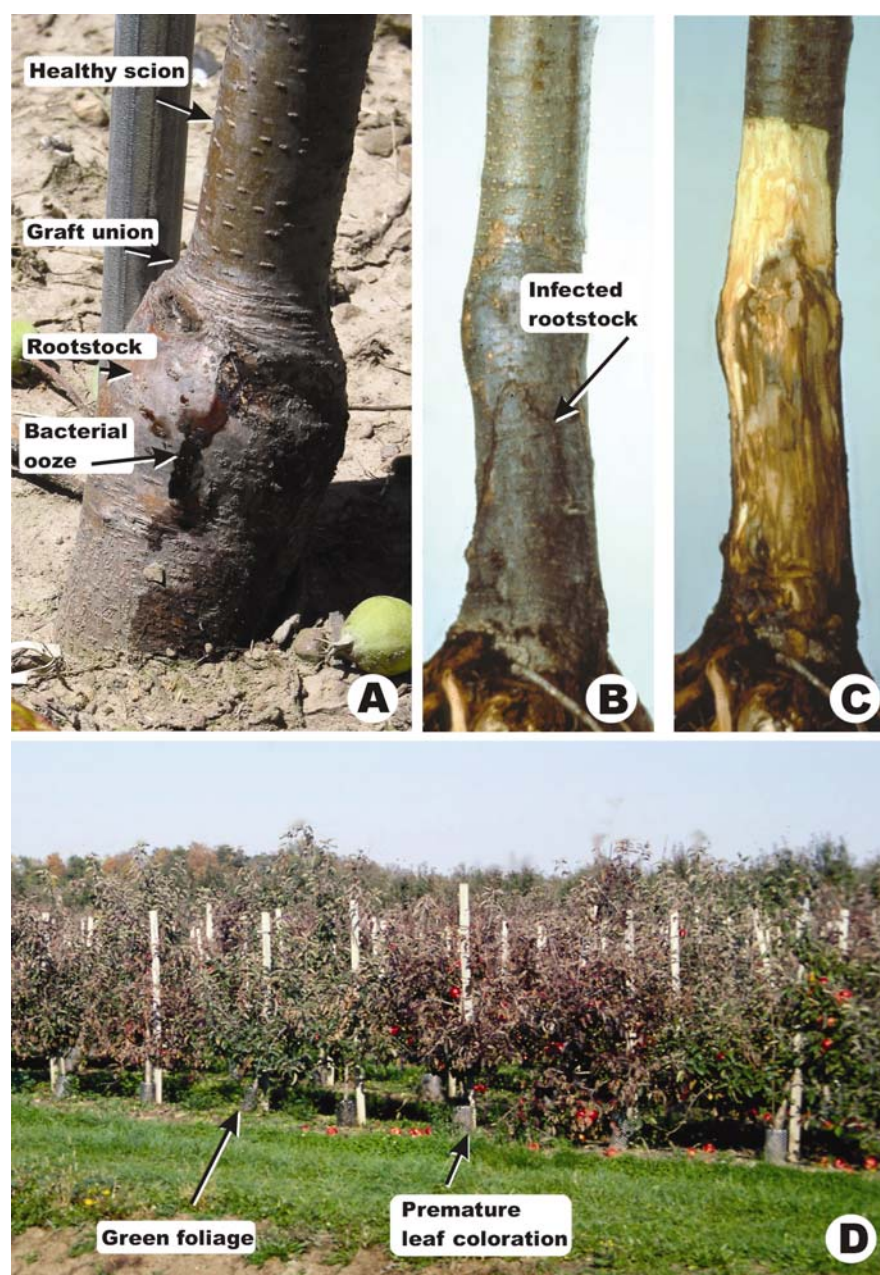


Fig. 3. Rootstock blight is characterized by the presence of liquid bleeding (bacterial ooze) from the rootstock in early summer (A) and by necrosis (B) that is more visible when the bark is removed (C). Trees with rootstock infection often exhibit yellow to burgundy foliage about a month before onset of normal autumn coloration (D).

timicrobial proteins to intercellular spaces is that these proteins may be more exposed to degradation by extracellular proteases. In *in vitro* assays of transgenic 'Galaxy' lines, attacin was partially degraded in the intercellular fluid of apple leaves (28). Using signal peptides fused to the protein (57), we demonstrated that intercellular localization of attacin significantly increased its efficacy in enhancing fire blight resistance (Fig. 5) (28). Transgenic 'Galaxy' lines with attacin fused to a signal peptide had a lower attacin content than lines without the signal peptide. However, transgenic 'Galaxy' lines transformed with attacin fused to a signal peptide had significantly less disease than those without the signal peptide, suggesting that intercellularly secreted attacin is more effective in reducing *E. amylovora* infection than intracellularly localized attacin.

From 1998 through 2001, 2- to 5-year-old trees of 'Royal Gala' and 'Galaxy' transgenic lines containing attacin, cecropins, and avian lysozyme were evaluated for fire blight resistance in several field trials. Many transgenic lines, especially those containing attacin, had significantly increased resistance to fire blight (42). Lines with higher attacin content had significantly decreased disease. Many of the lines initially identified in 1998 as resistant have continued to show resistance in several years of field tests. Flowering and fruiting have been evaluated since 1999. All transgenic fruits have been graded for size and color, pressure tested for firmness with and without skin, and assayed for soluble solids and titratable acidity and found to be statistically indistinguishable from fruit of 'Royal Gala' from nontransformed trees growing in the same rows.

Recent genetic engineering research has emphasized promoting plant defense responses to infection by *E. amylovora*, rather than introducing antimicrobial proteins not normally present in apple that act directly against the fire blight pathogen. *E. amylovora* produces the effector protein harpin, which induces resistance to fire blight when applied topically to apple flowers (5). Some M.26 lines transformed with the harpin gene (*hrpN*) driven by the *gst1* pathogen-inducible promoter were shown to have increased fire blight resistance in growth chamber and in preliminary field tests. The NPR1 protein, cloned from *Arabidopsis thaliana*, is thought to be a key regulator in the induction of plant disease resistance, and when this protein is over-expressed, it has increased broad spectrum disease resistance in *Arabidopsis* and rice (11,12). Sheng-Yang He, Michigan State University, cloned the apple homolog, *MpNPR1*, which we transferred to M.26 and 'Galaxy'. In preliminary growth chamber assays, some *MpNPR1* transgenic lines appear to have increased resistance to fire blight. *E. amylovora* secretes the DspE

pathogenesis factor, whose interaction with proteins in apple is thought to be necessary for fire blight disease to develop. Four DspE-interacting kinases have been identified and sequenced in the laboratory of our Cornell University colleague, S. V. Beer (35). Sense sequences have recently been transferred to M.26 with the goal of silencing the kinases and preventing disease development.

Although the results described here have provided good evidence of the feasibility of genetically engineering apple for increased resistance to fire blight, the transgenic lines produced thus far are all experimental. It is unlikely that many of these transgenic lines will be further developed for commercial use because of regulatory hurdles associated with the particular genes, especially several of the anti-

microbial proteins. Different genes, promoters, and regulatory sequences from those described here will likely be incorporated into transgenic lines designed for use in commercial apple growing. Altering the expression of native apple genes to increase fire blight resistance will probably present fewer regulatory issues and be more acceptable to growers and consumers. Before being commercialized, transgenic apple cultivars, like other crops, will go through rigorous "deregulation" (i.e., approval) requirements to demonstrate their safety for consumers, the environment, and agriculture.

Resistant Rootstocks from Conventional Plant Breeding

The increasing severity of fire blight in apple plantings on M.9 and M.26 rootstock

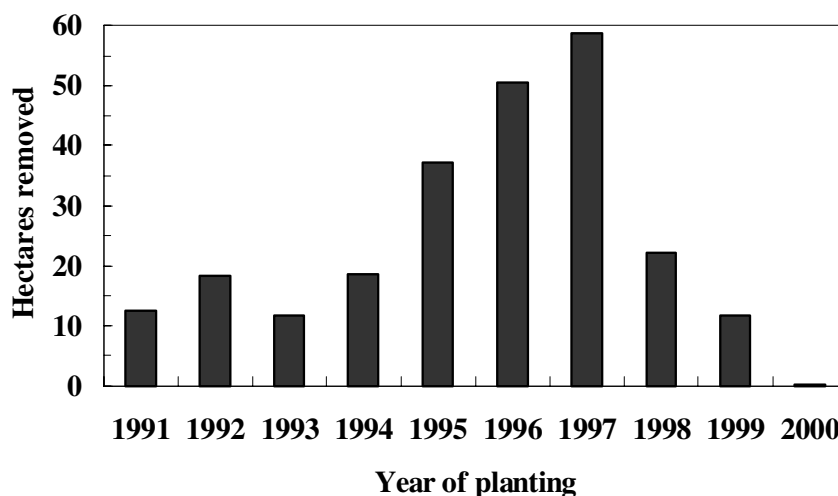


Fig. 4. Age distribution (planting year) of apple orchards removed following a severe fire blight epidemic in southwestern Michigan in 2000. About 240 ha (600 acres) of apple orchards were removed in the fall of 2000 and spring of 2001, primarily due to fire blight infection (data from USDA National Agricultural Statistics Service).

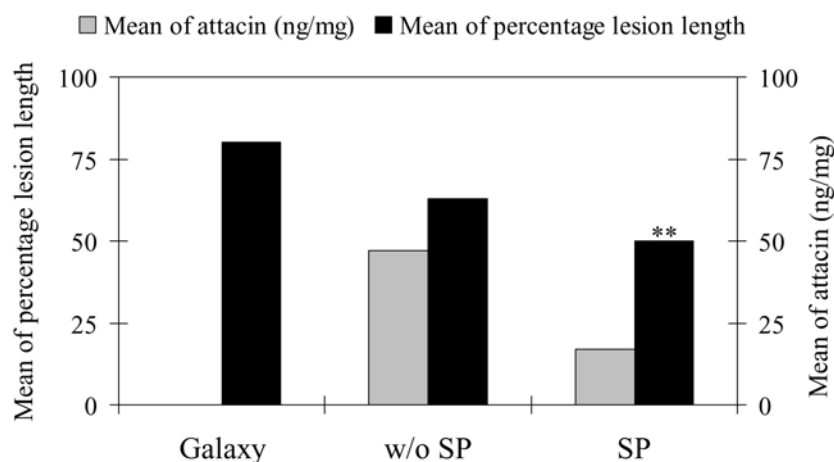
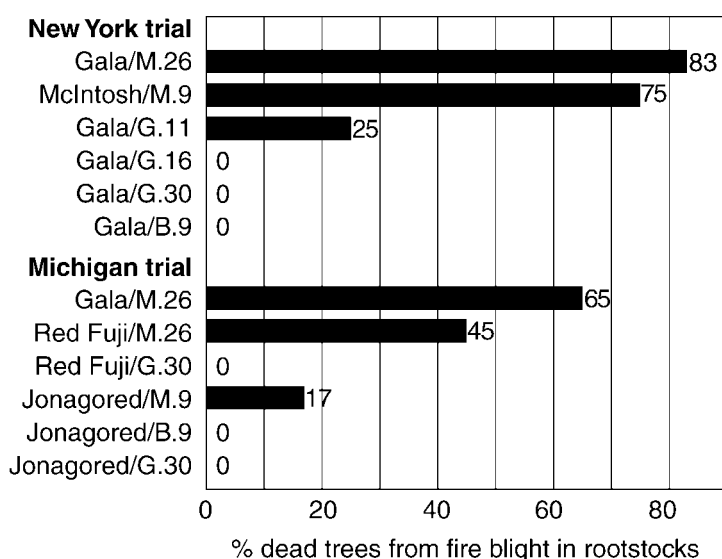


Fig. 5. Attacin content and fire blight resistance of nontransgenic 'Galaxy' (Galaxy), attacin-transgenic 'Galaxy' lines without signal peptides (w/o SP), and attacin-transgenic 'Galaxy' lines with signal peptides (SP). Signal peptide fused to the attacin protein results in transport of attacin to intercellular space. Although lines with signal peptides contained less attacin, they were significantly ($P = 0.01$) more resistant to fire blight. Reprinted with kind permission of Kluwer Academic Publishers from Ko et al. 2000. Biotechnol. Lett. 22:373-381 (original Figure 4) (28).

Table 1. Horticultural characteristics and commercial availability of apple rootstocks resistant to rootstock blight under orchard conditions

Rootstock	Tree size	Horticultural characteristics		2003 Commercial availability
		Strengths	Concerns	
B.9	M.9	Equal to M.9 in precocity, yield efficiency and fruit size. Most widely tested of resistant rootstocks in NC-140 and grower trials (32).	Although orchard trees on B.9 have been resistant to rootstock infection, basis of resistance is not understood. Sensitive to <i>Tomato ringspot virus</i> , susceptible to woolly apple aphid.	Most commercial nurseries supply trees on B.9.
G.16	M.9	Production equals M.9, very early bearing. Resistant to <i>Phytophthora</i> .	Limited orchard trials to date. Susceptible to common latent viruses, difficult to propagate, and susceptible to woolly apple aphid.	Limited availability of trees; 100,000 rootstock liners available for sale to nurseries.
G.30	M.26 to M.7	Much more precocious than M.7 (similar to M.26). High productivity in NC-140 and grower trials.	Many spines in stoolbed, requires extensive hand labor resulting in high tree production costs. Requires trellis support due to brittle graft unions with some cvs., e.g., 'Gala'.	Limited availability of trees; 50,000 to 80,000 rootstock liners available for sale to nurseries.
G.11	M.9 to M.26	More productive than M.26.	Only moderately resistant to fire blight. Susceptible to replant disease and woolly apple aphid.	Should be available in 2004.
G.202	M.26	Woolly apple aphid resistant. More productive than M.26. Propagates well in stoolbed.	Has not been evaluated in the United States. Only moderately resistant to fire blight.	Available only in New Zealand. Will be released in the United States in 2004.

Cultivar/rootstock combination**Fig. 6.** Frequency distribution of trees with rootstock blight following inoculation of the scions with *Erwinia amylovora*. Similar trials were conducted in New York (43) and Michigan (27). Blossoms were inoculated during bloom on the trees in the New York trial, while a single shoot in each tree was inoculated on the trees in Michigan. In both trials, rootstock blight was severe on M.26 and M.9 and absent on B.9 and G.30.

has made the development of fire blight resistant rootstocks a priority in rootstock breeding. Although resistant rootstocks do not prevent fire blight infection of susceptible scion cultivars, they do prevent tree losses resulting from rootstock infection (Fig. 3). Because quality of their fruit is irrelevant to the performance of rootstocks, fire blight-resistant apple rootstocks have been developed by conventional breeding much more quickly than have apple scion cultivars. The Geneva (United States) and Vineland (Canada) breeding programs have recently released rootstocks that were selected for resistance to fire blight (13,15).

In addition, Budagovsky (B.) 9 and some of the Japanese rootstocks that were not initially selected for fire blight resistance have been reported to be either tolerant or resistant to fire blight (4,21). New apple rootstocks having desirable pomological characteristics combined with resistance to infection by *E. amylovora* may provide practical control for the rootstock phase of fire blight in the near future (Table 1).

The objective of the Geneva apple rootstock-breeding program has been to develop pomologically superior rootstocks with resistance to abiotic and biotic stresses, including fire blight. *Malus* ×

robusta 'Robusta 5' and *M. × sublobata* PI286613 ('Novole') were identified as highly resistant to *E. amylovora* and have been widely used as parents in the Geneva rootstock breeding program (23). 'Robusta 5' and 'Novole' were later found to be differentially susceptible to specific strains of *E. amylovora*, but when rootstock selections were inoculated with a mixture of highly virulent strains, it was possible to select rootstocks with resistance to most *E. amylovora* strains in a nondifferential manner (39,40,43,54). Resistance effective against strains of different virulence patterns (or races) should be more durable than resistance selected against a single strain. By 1994, the Geneva program had produced and evaluated approximately 350,000 seedlings resulting from controlled crosses (15). To date, four apple rootstocks, Geneva (G.) 65, G.11, G.30, and G.16 have been released for commercial sales, and several other selections are in the final stages of evaluation (15). In 1998, the Geneva program became a joint USDA-ARS/Cornell effort aimed at the continued development and evaluation of new apple rootstocks.

Similarly, the goals of the rootstock breeding program at the former Horticultural Research Institute (HRI) of Ontario at Vineland Station were to develop rootstocks that were easily propagated, winter hardy, and resistant to common pests, including fire blight (13,14). Although the breeding program has been discontinued, evaluation and commercial development of the material produced is continuing. Several of the Vineland (V) rootstocks, including V.1, V.2, V.4, and V.7, have been reported to be resistant or tolerant to fire blight (13,20,21).

The Geneva rootstocks have been evaluated for their resistance to *E. amylovora*

when used as rootstocks of fruiting trees in trials conducted in New York and Michigan (Fig. 6) (27,43). Rootstocks can become infected by internal spread of bacteria from infections in the scion, by infection of rootstock suckers (vegetative shoots developing from the rootstock), or by infection through gaps in rootstock bark caused by growth or various injuries (38). In both the New York and Michigan trials, blossoms or shoots on the scion cultivar were inoculated to provide an inoculum source for the various avenues of infection. The development of rootstock blight was evaluated based upon the presence of bacterial ooze on rootstocks or typical fire blight necrosis of the rootstock tissue, and by the observation of either tree death or premature leaf coloration in the fall (Fig. 3). Trees on G.16, G.30, and B.9 were highly resistant to rootstock infection (no tree mortality), in comparison with M.9 and M.26 rootstock clones. Orchard trees on G.11 were moderately resistant to rootstock infection (25% tree mortality).

V. I. Budagovsky from the Michurin College of Horticulture, Michurinsk, Russia, introduced B.9 in 1962 (10,14). B.9 was not originally selected for resistance to *E. amylovora*, and the failure of trees on B.9 to develop rootstock blight in both the New York and Michigan trials (Fig. 6) was unexpected because B.9 itself is highly susceptible to fire blight when shoots of own-rooted plants are inoculated in a greenhouse (43). The reasons for this contradiction between the susceptibility of B.9 as an inoculated liner in the greenhouse, and the resistance of B.9 when used as a rootstock for flowering, grafted orchard trees, is not understood. However, replicated field trials conducted in Ohio showed a high level of resistance of B.9 to rootstock blight in comparison to orchard-grown trees of M.26 and M.9, which consistently had a high level of tree loss (19,20,21). In addition to B.9, Ferree et al. reported a greater percent of trees on Poland 1, Poland 2, V.1, V.4, V.7, B.491, and B.469 rootstocks surviving natural infections of fire blight in Ohio orchard trials when compared with M.9 and M.26 (20).

New Chemical Technologies for the Control of Shoot Blight

There is a critical need for new effective materials for managing blossom and shoot infections because in many apple growing areas *E. amylovora* has developed resistance to the most effective material, streptomycin. Although the need for effective chemicals is more pressing than ever, new antibiotics have not been registered for fire blight control in recent years (34) and biological control agents work best when their use is integrated with the use of antibiotics (50). Other antibiotics (e.g., gentamycin), synthetic chemicals (e.g., oxolinic acid), and biological control agents (e.g., *Bacillus subtilis* QRD-137, *Pseudomonas fluores-*



Fig. 7. Effect of prohexadione-calcium (Apogee) on shoot growth and fire blight. Three-year-old 'York' trees on M.26 rootstock were either not treated (A and B) or treated with 250 mg of prohexadione-calcium per liter applied at 5 to 8 cm of shoot growth and 125 mg of prohexadione-calcium per liter applied 15 days later (C and D). Inoculation of a subset of trees with *Erwinia amylovora* 13 days after the final prohexadione-calcium application resulted in 99% of the current season's shoot length blighted (SLB) in nontreated trees (B) and 5% SLB in treated trees (D). Each colored section of height marker is 30.5 cm. Photographs courtesy of Stephen Miller, USDA-ARS, Appalachian Fruit Research Station, Kearneysville, WV.

cens A506, and *Pantoea agglomerans* C-91) have shown potential in some field trials. Another interesting area of our research has been on materials that increase the resistance of apple tissues to infection by inducing host resistance, without affecting the pathogen directly.

Growth retardants. Prohexadione-calcium (Apogee) is a plant growth regulator that reduces longitudinal shoot growth by inhibiting gibberellin biosynthesis (45). On apple, controlling vegetative growth with prohexadione-calcium also reduces the incidence and severity of fire blight shoot infection (61) (Fig. 7). Prohexadione-calcium does not exhibit antibacterial activity against *E. amylovora* but increases host

resistance by reducing plant vigor. In addition, treatment of apple with prohexadione-calcium results in alteration of phenylpropanoid biosynthesis pathways that may also enhance resistance (18). Modifying the susceptibility of apple trees to fire blight with plant growth retardants offers greater flexibility than attempting to modify susceptibility with common horticultural practices such as varying the levels of fertilization, pruning, and fruit thinning. Reducing shoot lengths should also reduce the need for annual pruning and improve light penetration into the center of apple trees.

Prohexadione-calcium is applied near the end of bloom when the petals on the

king (first, central) blooms become senescent and dehiscence (Fig. 8). The length of time that shoot growth is inhibited depends not only on application rate of prohexadione-calcium but also on tree vigor (26). A single well-timed treatment will visibly suppress shoot elongation within 2 weeks after application and, under the growth conditions present in Michigan and New York, the suppression is maintained until the threat of fire blight has subsided. In regions where growth extends later into the summer than in the northeastern United States, suppression can be maintained with additional applications of prohexadione-calcium.

Trials in Michigan in 1999 and 2000 demonstrated the ability of prohexadione-calcium to control fire blight under severe natural infection conditions (Fig. 9). Prohexadione-calcium was applied at petal fall either as a single spray or as two sprays, with the total amount of chemical applied per hectare being the same. Storms with high winds and rain occurred shortly after petal fall in both seasons and contributed to the high level of natural infection in these trials on unsprayed trees. The level of control under these severe conditions was 60 to 75%. In 1999, both single and split ap-

plications of prohexadione-calcium significantly reduced the amount of blossom and shoot blight. In 2000, a single application significantly reduced blossom and shoot blight, and was more effective than the split application where the level of control did not differ from unsprayed trees.

Field trials in Virginia have validated the use of prohexadione-calcium for suppressing fire blight outbreaks in grower orchards (60). Hail injury occurred in five of 10 orchards in 2001 where replicated trials were established to demonstrate the value of prohexadione-calcium for suppressing fire blight. In June and early July, incidence of shoot blight on trees treated with prohexadione-calcium was reduced by 88 to 96% in the four orchards where fire blight occurred. An examination of these trees in autumn indicated a reduction of 61 to 96% in potential overwintering cankers on the prohexadione-calcium treated trees compared to control trees.

Trinexapac-ethyl (Moddus, Palisade), another compound known to inhibit gibberellin biosynthesis and currently used to protect cereal crops against lodging, can also retard shoot growth in apple trees and suppress the secondary spread of fire blight (27). Although more work needs to be done

with this material and related compounds, eventually a range of shoot growth inhibitors should be available for use in fire blight control programs. Interestingly, transgenic apple lines have been produced at HRI, UK, in which the G-20 oxidase enzyme (a step in gibberellic acid biosynthesis) has been silenced, and these lines will be evaluated at Geneva, NY, for effects on fire blight resistance.

Systemic acquired resistance (SAR) inducers for fire blight control. Acibenzolar-S-methyl (ASM, Actigard, BION) stimulates the tree's natural defense mechanisms through the SAR pathway. ASM provided a significant level of fire blight control under very favorable conditions for fire blight infection in Michigan in 1999 and 2000 (Fig. 10) and in studies conducted in Europe (9).

ASM stimulates the expression of pathogenicity related protein (PR) genes in tobacco (22), wheat (24), and *Arabidopsis* (29), and a similar response was also detected in apple (9,33). Genes associated with SAR in herbaceous plants, such as PR-1, PR-2, and PR-8, were also identified in apple and exhibited a significant increase in expression 3 to 5 days after treatment with ASM.

Applications of SAR-type compounds need to be made before infection occurs, to allow sufficient time for the induction of resistance (Fig. 11). In most trials, ASM treatments were initiated at the pink stage of bud development, which is about a week before the first streptomycin applications might be applied. The effectiveness of the resistance induced by ASM against *E. amylovora* does not appear to last as long on apple as reported for pathogens of some herbaceous plants. The best control of blossom blight and terminal infections with ASM was obtained when sprays were repeated weekly rather than biweekly (Fig. 10) (33). The effectiveness of ASM for shoot blight control increased as treatment rates were increased; for each application, a rate of 75 to 100 mg a.i./liter may be adequate. Although multiple applications of ASM reduced the incidence and severity of fire blight, it was not nearly as effective as streptomycin.

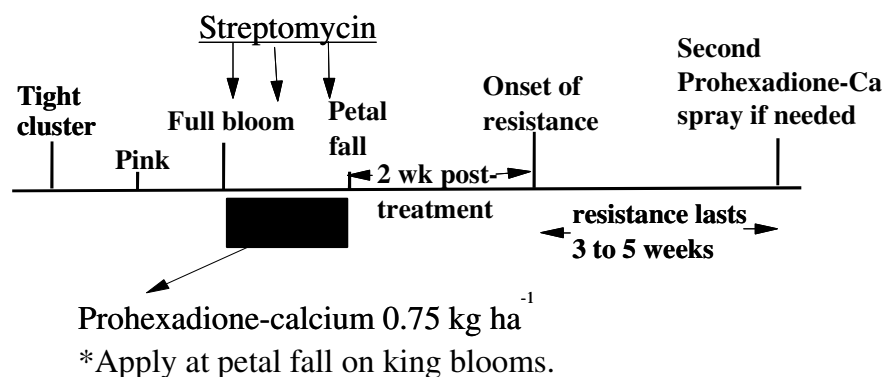


Fig. 8. Schematic diagram of a fire blight management strategy based upon applications of prohexadione-calcium (Apogee) and streptomycin. Streptomycin is used for controlling blossom blight, while prohexadione-calcium controls vegetative growth, thus inhibiting secondary spread of fire blight. Prohexadione-calcium is usually applied with a suitable wetting agent (such as Regulaid), and ammonium sulfate is sometimes included in the tank mix, depending on the formulation and water hardness. A forecasting system such as MaryBlyt or Cougarblight is used to predict fire blight infection periods and to determine the requirement for and optimum timing of streptomycin sprays.

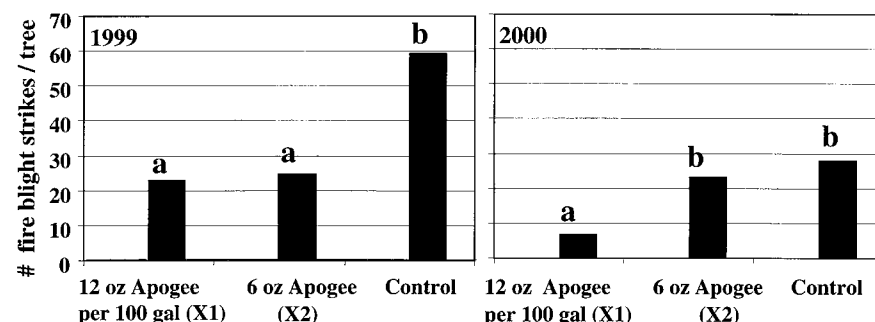


Fig. 9. Fire blight strikes on trees sprayed once (X1) or twice (X2) with prohexadione-calcium (Apogee) in 1999 and 2000. Data are for natural infections and do not include inoculations to selected blossom clusters in each tree to ensure the presence of inoculum. Letters indicate statistical significance ($P = 0.05$) according to an LSD test.

Outlook for the Future

Effective fire blight management will continue to rely on an integrated approach combining several disease control strategies. Because of the development of resistance to streptomycin in *E. amylovora* in many areas, and the debate concerning the use of antibiotics in agriculture (34), our research goal has been to find alternative fire blight control practices that could replace streptomycin in the future. This goal has yet to be achieved. However, new technologies that enhance host resistance to fire blight have advanced significantly in the past decade and hold promise for the future.

Prohexadione-calcium is now registered in the United States for the suppression of fire blight on apple. Once prohexadione-calcium received an Environmental Protection Agency (EPA) registration, large-scale trials in grower orchards were conducted to verify the efficacy observed in small-scale trials and to establish commercial applicability (60). Because prohexadione-calcium suppresses tree growth, its use is most appropriate in established orchards, and it may not be of value in young orchards where tree growth is important for developing productive trees. However, tree losses from fire blight are usually most devastating in young (2 to 5 year old) orchards (Fig. 4). Prohexadione-calcium must be applied 2 to 3 weeks before the normal period of shoot infection and before the effectiveness of blossom blight control sprays can be evaluated (Fig. 8), so the expense of prohexadione-calcium applications may not be recovered in years when fire blight is not a significant problem. However, as an orchard management tool, the economic benefits of prohexadione-calcium applications may be realized through its effect on growth suppression (reduced pruning costs, improved fruit quality, improved spray coverage, etc.).

The development of prohexadione-calcium has advanced our ability to control shoot blight, but effective blossom blight control still requires the use of streptomycin (Fig. 8). Streptomycin is even more important to the pear industry because prohexadione-calcium is currently only registered for use on apples. SAR inducers evaluated for fire blight control cannot yet be considered as replacements for streptomycin. Although the results are encouraging, they have not exhibited a sufficiently high level or consistency in efficacy to justify their use in place of streptomycin for the management of fire blight (Fig. 10). However, understanding the physiological and molecular basis for how these compounds control fire blight should lead to even better approaches for fire blight management in the future.

The promise of genetics to reduce the severity of damage caused by fire blight infection is now beginning to be fulfilled, as rootstocks bred specifically for resistance to fire blight are being introduced into the apple industry. These rootstocks generally have good to excellent horticultural performance, and their fire blight resistance has in many cases been confirmed in field trials (46). However, as with all new apple cultivars developed by breeding, the heterozygosity of apple inevitably leads to unexpected characteristics that may be deleterious in the nursery or orchard. Multi-year trials in different regions are required to reveal these problems and determine whether the advantages of the new rootstock outweigh the novel problems. We are optimistic that some fire blight-resistant rootstocks will eventually

emerge as effective solutions to rootstock blight.

Breeding of fire blight-resistant scion cultivars is less promising. However, there is now convincing evidence that fire blight-resistant strains of existing commercial cultivars can be produced by genetic engineering. Although some of the genes used in the initial "proof of concept" phase of this research are unsuitable for use in commercial apple production, some other genes have clear potential for commercial application. Besides genes with direct antimicrobial activity, constructs altering the expression of native apple genes, by over-expressing genes involved in host resistance or silencing genes involved in pathogenesis, appear to have great potential for commercial use. Acceptance of transgenic apple cultivars by those concerned about their food and environmental impact will

be facilitated by current research to use selectable markers that do not rely on antibiotic resistance, and to excise transgenes from mature fruit and pollen.

This article has focused on recent progress in the development of new fire blight control technologies that enhance host resistance by chemical or genetic means. These technologies are compatible with existing fire blight management practices aimed at reducing inoculum levels in the orchard and interfering with the infection process. Apogee is currently available for use, and the Geneva rootstocks should be useful in the near future. Other technologies, such as transgenic cultivars and SAR inducers, require more research and are further down the road. Because they are new, it is premature to claim that any of these specific technologies will be widely adopted by the apple industry. However, as

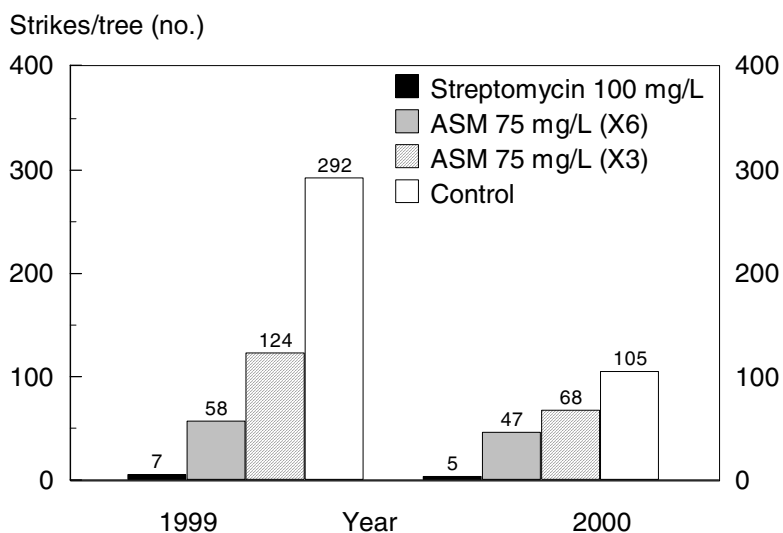


Fig. 10. Fire blight strikes per tree on Jonathan apple trees inoculated with *Erwinia amylovora*. Two acibenzolar-S-methyl (ASM, Actagard 50 WG, Syngenta) treatments were initiated 1 week pre-bloom, and successive sprays were applied on a 7- or 14-day interval that resulted in a total of 6 (X6) or 3 (X3) applications, respectively. Streptomycin (Agrimycin 17, Syngenta) was applied twice during bloom and then on a 7-day interval. Storms with high wind and rain occurred shortly after petal fall both seasons and contributed to the high level of natural infection observed in these trials on unsprayed trees. Reprinted from Maxon-Stein et al. 2002. Plant Dis. 86:785-790 (33).

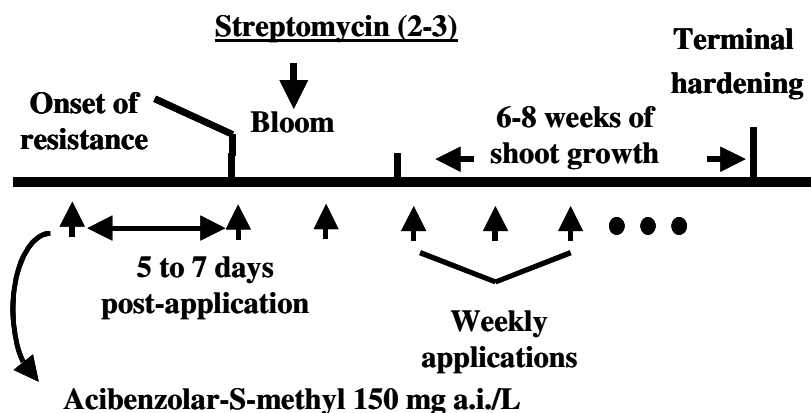


Fig. 11. Proposed management strategy that integrates uses of acibenzolar-S-methyl (ASM) with streptomycin for fire blight control. Streptomycin is used for controlling blossom blight, while ASM is used to boost the natural resistance of apple trees to fire blight. Necessity for streptomycin sprays is determined with a fire blight forecasting system such as MaryBlyt or Cougarblight.

our understanding of host resistance mechanisms continues to advance, technologies for enhancing host resistance will add a new dimension to fire blight control in the twenty-first century.

Acknowledgments

This research was supported in part by USDA/CSREES special grants to Michigan and New York, by Michigan and New York Apple Research Committees, and by Agricultural Experiment Stations in Michigan and New York. We thank Wilbur Hershberger, USDA-ARS, for assistance in preparation of figures. We also thank Marty Saffell, United States Department of Agriculture, National Agricultural Statistics Service, for providing the tree loss survey data for the 2000 epidemic and Mark Longstroth for help in summarizing the data.

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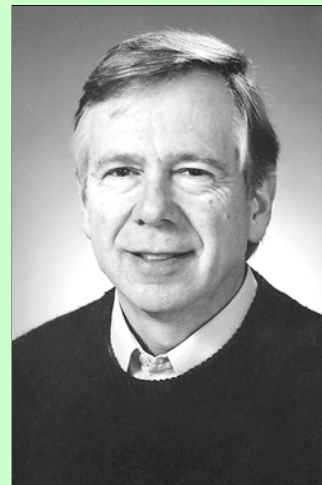
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